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# NOTES AND LITERATURE

## THE CLASSIFICATION OF THE LIVERWORTS

BOTANISTS have long felt that the classification of the liverworts was very much in need of revision, and any serious attempt to establish a classification that will better express the real inter-relationship of the Hepaticæ is very welcome. The valuable series of papers recently published by Dr. Cavers,[1] on the classification of the Bryophytes, is a distinct contribution to the subject, and is a decided advance over any classification that has been proposed hitherto.

Dr. Cavers is well known to students of the liverworts through a series of papers of exceptional merit, published at intervals during the past few years. The present publication presents at length the conclusions he has reached as a result of his studies on these important plants.

It is still too early to expect a definitive classification of the liverworts, as there are still a good many important types whose development is incompletely known, and it is also highly probable that there are still forms awaiting discovery which we may reasonably expect will throw light upon some relationships which are still obscure.

Dr. Cavers has made a careful study of the work of the most recent investigators, as well as of the older standard works, and while one may take exception to a few of his deductions, still, as a whole, one will agree with his main conclusions, and will welcome this contribution of his as a decided advance in our knowledge of the inter-relationships of the Bryophytes. The Bryophytes (or "mosses," using this term in its widest sense) are forms of peculiar interest to students of plant-morphology, especially to those engaged in the problems of the origin of the higher types of plants; since the Bryophytes occupy an intermediate place between the aquatic algæ and the ferns which are typically land plants. While there is decided difference of opinion as to how the ferns originated, the weight of evidence is strongly on the side of their direct derivation from some liverwort-like ancestor. It is this question that makes a thorough study of the liverworts of such great importance in seeking for an explanation of the origin of the vascular plants.

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[1] "The Inter-relationships of the Bryophyta," by Frank Cavers, D.Sc., F.L.S. (*New Phytologist*, Reprint No. 4), Cambridge; at the Botany School, 1911.

Aside from this, however, the Bryophytes, especially the liverworts or Hepaticæ, are exceptionally interesting, as they show in a remarkably clear way many adaptations to special environmental influences.

The Bryophytes are divided, usually, into two main groups—the Liverworts (Hepaticæ), and the True Mosses (Musci). One peculiar order, Anthocerotales, the "Horned Liverworts," is sometimes considered to represent a third class, coordinate with the Musci and Hepaticæ. Cavers does not accept this view, but considers them to represent an order only of the Hepaticæ.

Aside from the Anthocerotales, the liverworts usually are divided thus into two orders, Marchantiales and Jungermanniales. There are, however, several genera that to a certain extent combine characters of both of these orders and sometimes have been assigned to one, sometimes to the other. Of these genera *Sphærocarpus* may be cited. This is, on the whole, probably the simplest known liverwort, and is represented in the United States by several species in the warmer parts of the country. Much like *Sphærocarpus* is a peculiar liverwort, *Geothallus,* known as yet only from San Diego in Southern California. A third genus, *Riella,* evidently related to these, is an aquatic type, only recently found in America. All of these are very simple liverworts and probably stand near the base of the liverwort series. They may, perhaps, be regarded as synthetic types connected with both of the main series of liverworts. Cavers proposes to unite them into a special order, Sphærocarpales, and this conclusion will probably be accepted as representing best their position in the system. In the Sphærocarpales, as interpreted by Cavers, the sporophyte or neutral generation is of simple structure, and the elaters which in the typical liverworts accompany the spores are represented by undifferentiated sterile cells.

From some form probably not very unlike *Sphærocarpus,* but with perhaps a still simpler sporophyte, it is probable that the two lines of development, the Marchantiales and the Jungermanniales have diverged. Within these two orders the course of development can be easily traced, as nearly all the stages in the evolution of the two groups are represented by existing genera. It is hard to say which of the two orders should be considered the more primitive, as the lower members of each are of about equal complexity, and can be derived equally well from some form allied to *Sphærocarpus.*

*Sphærocarpus* has been associated most commonly with the Ricciaceæ, the lowest of the Marchantiales, but there are certain genera of the Jungermanniales that in many ways show a close resemblance to the Sphærocarpaceæ, and make it almost certain that there is a real relationship existing between them. These similarities are found both in the character of the thallus and reproductive organs, as well as in the early history of the embryo. They may be only cases of parallel development, but it is quite as likely that they are true homologies. Two genera, *Petalophyllum* and *Fossombronia,* which have always been placed in the Jungermanniales, are especially suggestive of a possible connection with the Sphærocarpales, and it is by no means impossible that it may turn out that these genera, and possibly some others, should be removed from their association with the Jungermanniales and transferred to the Sphærocarpales.

## THE MARCHANTIALES

The Marchantiales constitute a very natural order, whose simplest members, the Ricciaceæ, are sometimes separated as a distinct order. There does not seem to be any valid reason for this, however, as the Ricciaceæ are connected with the more highly specialized Marchantiaceæ by a number of intermediate forms.

The Marchantiales are comparatively few in number, probably not more than three hundred species being known; but their relatively large size and characteristic appearance make them the most conspicuous of the liverworts, the common and widespread *Marchantia polymorpha* being the most familiar liverwort to most students of botany. The dichotomously branched thallus, with its elaborate systems of tissues, probably may be said to represent the highest type of a strictly thallose plant.

Within the Marchantiales are many interesting cases of adaptation, and a very complete series of forms exists showing the evolution of the elaborate and highly specialized thallus of *Marchantia* and similar genera, from the much simpler type found in *Riccia*. The elaboration of the sporophyte can also be followed. *Riccia,* as is well known, has the simplest known sporophyte, in this respect being in a much lower plane than *Sphærocarpus,* although the thallus in the latter is much less specialized than in *Riccia.*

The evolution of the sporophyte, as every botanist knows, is associated with a reduction in the amount of tissue devoted to spore-production, and a corresponding increase in the purely vegetative or sterile tissue of the sporophyte. The latter, however, in the Marchantiales always remains relatively simple in structure.

In the lower Marchantiales the sexual organs are borne upon the dorsal surface of the unmodified thallus, but in the more highly specialized types like *Fimbriaria* or *Marchantia,* characteristic receptacles are developed, usually composed of a number of very short branches resulting from the repeated dichotomy of the original thallus apex. The classification of the Marchantiales has been based largely on the character of the receptacle and the sporogonium.

Cavers recognizes five families of very unequal size, viz., Ricciaceæ, Corsiniaceæ, Targioniaceæ, Monocleaceæ and Marchantiaceæ. The latter, which aside from the Ricciaceæ, comprises the greater part of the Marchantiales, was divided by Leitgeb into three subfamilies, Astroporæ, Operculatæ and Compositæ, but it is very doubtful whether these can be maintained.

The Ricciaceæ, the great majority of which belong to the genus *Riccia,* are undoubtedly the simplest, and probably the most primitive, members of the order. The extremely simple sporophyte is almost entirely devoted to spore production, there being no sterile tissue beyond a very imperfect single outer layer of cells. No other liverworts approach the Ricciaceæ in the simplicity of the sporophyte.

The second family, Corsiniaceæ, is intermediate in the structure of the sporophyte, between the Ricciaceæ and the higher Marchantiales.

The third order, Targioniaceæ, includes the two small genera, *Targionia* and *Cyathodium.* These are very characteristic liverworts represented in the United States by a single species *Targionia hypophylla,* common in the coast region of California, but absent from the eastern states. This species occurs also in southern and western Europe. *Cyathodium* includes a few species of delicate liverworts inhabiting dark crevices in rocks, or shallow caves. All the species show evidences of marked structural modifications due to their unusual habitat. *C. fœtidissimum* is a characteristic species of the Indo-Malayan region.

The simple genus *Monoclea* with two species represents very distinct the family Monocleaceæ. In his great work on the Hepaticæ, Leitgeb referred *Monoclea* to the Jungermanniales, and this view was adopted by Schiffner in his treatment of the Hepaticæ in Engler & Prantl's "Natürliche Pflanzenfamilien." This association with the Jungermanniales was mainly on account of the structure of the thallus, which is quite destitute of the air-chambers which distinguish most of the Marchantiales. There is also in *Monoclea* no definite archegonial receptacle, and the solitary sporogonium has a long seta like that of many Jungermanniales.

All the more recent students of *Monoclea,* however, are agreed that the plant really belongs to the Marchantiales, this being shown both by the structure of the thallus, and that of the reproductive organs. The absence of air-chambers is with little question to be looked upon as a secondary condition, due to the semi-aquatic habit of the plant. A similar disappearance of the air-chambers is known in the unmistakable marchantiaceous genus *Dumortiera.*

Leitgeb, in his important memoirs on the Hepaticæ, recognized three types of archegonial receptacle. Only in one of these was the receptacle compound in its structure. More recent studies, including those of Cavers, indicate that this compound or "composite" type is much more general than Leitgeb supposed. Cavers states that probably all of the genera of the Marchantiaceæ, except *Clevea* and *Plagiochasma,* will be found to have receptacles of the composite type.

In tracing the phylogeny of the Marchantiales, Cavers distinguishes two main divergent groups which are connected with the Ricciaceæ by *Corsinia* and *Boschia,* respectively. The first series includes, among other genera, *Clevea, Plagiochasma, Reboulia* and *Fimbriaria,* the latter representing the culmination of this series.

The second series, starting with *Boschia,* shows two main branches, one including the Targioniaceæ and *Monoclea,* the other the most highly developed genera, like *Fegatella, Dumor-*

*tiera* and *Marchantia.* The latter genus is the most highly specialized of all the Marchantiales.

### THE JUNGERMANNIALES

Much the greater number of liverworts belong to the Jungermanniales. The classification of this large order is very much in need of revision, as it is at present in a very unsatisfactory condition.

They are generally divided into two series of very unequal size, this division being based upon the position of the archegonium—and are denominated the Anacrogynæ and Acrogynæ. In the former the growing point of the shoot persists indefinitely, while in the latter, in the fertile shoots, it is sooner or later transformed into an archegonium, and the sporogonium is therefore terminal.

The name Metzgeriaceæ was later proposed by Underwood, as a substitute for Leitgeb's Anacrogynæ, the Acrogynæ being alone called Jungermanniaceæ. Cavers thinks these two divisions are largely artificial, and it must be admitted that there is much to be said for his view.

Comparing the Jungermanniales, as a whole, with the Marchantiales, it is seen that in the former specialization has been in the direction of external differentiation, *i. e.,* in most of them a more or less definite axis, bearing leaves, is present, but the tissues remain quite uniform. In the Marchantiales, on the other hand, the plant is a thallus, but the tissues are of various kinds.

The simplest of the Jungermanniales, *e. g., Aneura, Pellia,* etc., have a very simple thallus, either composed of quite similar cells, or with a midrib which may possess a strand of special conductive tissue. The simplest type of thallus is quite like that of *Sphærocarpus,* and may very well have originated from some similar type.

In these thallose Jungermanniales there is frequently a tendency toward the development of marginal lobes, which may bear a quite definite relation to the primary divisions of the single apical cell of the thallus. Such marginal lobes are undoubtedly homologues of the leaves found in the more highly specialized leafy liverworts—the "Acrogynæ," of Leitgeb. Sometimes these leaf-like organs of the anacrogynous liverworts are very distinct, as in *Treubia,* and the transition to the typical leafy liverworts like *Porella* or *Frullania*, is a very gradual one. It is very clear that this tendency towards leaf-development has arisen in a number of quite disconnected genera, and this of course suggests a multiple origin for the Acrogynæ.

Cavers proposes four families of the lower, or anacrogynous, Jungermanniales, viz., Aneuraceæ, Blyttiaceæ, Codoniaceæ, Calobryaceæ. He thinks that the first three are more or less artificial, and it is very certain that it will be necessary when some of the less known genera are more fully investigated, to make a radical revision of these families. The Calobryaceæ, on the other hand, forms a sharply defined and natural family, comprising two genera, *Haplomitrium* and *Calobryum*. Cavers concludes that there are two main lines of development within the Anacrogynæ, one including the Codoniaceæ and Calobryaceæ, the other the Blyttiaceæ and Aneuraceæ, suggesting that the two latter families might perhaps be better united into a single one. There seems to be little question that the two families are closely related through such forms as *Umbraculum* and *Podomitrium*.

There is much uncertainty as to the limits of certain genera. This is especially the case with the genus *Calycularia*, to which have been assigned species which further investigation has shown to belong to quite different families. The writer has had occasion recently to examine carefully the structure of *Calycularia radiculosa*, a rare species from Java. Schiffner concluded that this species should be removed from the genus *Calycularia*, of the family Codoniaceæ, and united with *Mörkia*, a member of the Blyttiaceæ. While it is certainly distinct from the true species of *Calycularia*, it is equally certain that it can not be assigned to *Mörkia*. It will probably have to be separated into a distinct genus with characters intermediate between those of the Codoniaceæ and the Blyttiaceæ. In short, it is very clear that at present a satisfactory classification of the group is not feasible.

The Aneuraceæ and Blyttiaceæ show an interesting type of specialization of the thallus which is wanting in the Codoniaceæ and Calobryaceæ, where the tendency is toward the development of leaf-like lobes foreshadowing the leaves of the leafy liverworts. In *Podomitrium* and *Umbraculum*, assigned respectively to the Blyttiaceæ and Aneuraceæ, the thallus is differentiated into a prostrate cylindrical rhizome and erect dichotomously branched fan-shaped shoots, which resemble very closely the delicate leaves of certain filmy ferns, for which these liverworts might easily be mistaken.

In the development of the sporophyte the Anacrogynæ show a decided advance over the Marchantiales. There may be developed a considerable amount of sterile tissue in the capsule, aside from the ordinary elaters, and this sterile tissue sometimes assumes the form of a sort of columella or "elaterophore," suggesting the columella found in the Anthocerotaceæ, and possibly homologous with it. This elaterophore may be either apical (*Aneura*) or basal (*Pellia*).

While recognizing the entirely independent origin of leaves in several lines of the Anacrogynæ, nevertheless Cavers is inclined to believe that all of the true leafy liverworts (Acrogynæ) can be traced back to a single type which he thinks is best represented by *Fossombronia,* which genus he places at the top of the series Codoniaceæ. It may be said, however, that there are some strong arguments in favor of a polyphyletic origin for the Acrogynæ—a view which has been defended by several students of the group.

There are, as we have already stated, good reasons for believing that *Fossombronia* should not be associated with *Pellia* and the other Codoniaceæ, but associated with the Sphærocarpales, as the highest member of a series of which *Sphœrocarpus* and *Geothallus* are lower members. This interpretation would not interfere with the acceptance of Cavers's view that some at least of the leafy liverworts have been derived from forms like *Fossombronia.*

The acrogynous Jungermanniales, or leafy liverworts, include much the larger part of existing liverworts. Of about 250 genera and 4,500 species of known liverworts, all but 60 genera and 700 species belong to the acrogynous Jungermanniales. They are nevertheless comparatively uniform in type, and Cavers believes that they may all be traced back to a common ancestral type allied to *Fossombronia.*

With very few exceptions they show a single tetrahedral apical cell and usually three series of leaves corresponding to the three lateral faces of the apical cell. The ventral leaves (amphigastria) are not infrequently absent, and both dorsal and ventral leaves often show various modifications, among the most striking of which are hollow sacs presumably developed for water storage.

The tissues are very simple, and only very rarely is there any specialization of cells for conduction or other purposes. In size they range from almost microscopic forms like some of the minute epiphyllous Lejeuniaceæ, to stout species like some of the tropical *Frullanias,* which form pendant masses several feet in length.

In all the Acrogynæ the archegonia are in groups terminating the fertile branch, whose further growth is arrested by the transformation of the apical cell into an archegonium.

The sporogonium is always well developed, usually showing a well-marked foot and seta. Perfect elaters are always present. A small number only of the Acrogynæ have been studied critically with reference to the development of the sporophyte, and much more work must be done before the real affinities of some of the genera can be determined satisfactorily.

On the basis of our present knowledge of the group, Cavers proposes a classification based largely upon the work of Spruce. He recognizes two main divisions, the first including a single very large family, Lejeuniaceæ, with nearly 2,000 species; the second contains seven families, of which three, viz., Porellaceæ, Pleuroziaceæ and Radulaceæ, are regarded as natural families, the other four as more or less artificial, the limits between them being difficult to define.

The inter-relationships of the Acrogynæ are extremely difficult to follow. A number of students of the liverworts, notably Spruce and Schiffner, believe that the group is of polyphyletic origin, the Lejeuniaceæ representing a quite distinct line derived from forms allied to the Aneuraceæ. There are striking resemblances both of gametophyte and sporophyte, the former in some cases having a protonemal stage of long duration, and very much resembling one of the simpler thallose liverworts. Cavers believes, however, that these resemblances are simply parallel developments, and not true homologies; and, as already stated, that the Acrogynæ represent a single line of development. Of these forms he states that *Lophozia* probably comes nearer to the assumed ancestral type.

From the *Lophozia* type, three branches are traced, one through *Plagiochila* developing a large number of genera, among which *Cephalozia,* again, is the starting-point for the development of a number of specialized genera like *Zoopsis, Lepidozia,* and *Trichocolea.* The second line leads through *Marsupiella* and *Nardia* to a number of genera, of which the highest are *Stephaniella, Gyrothyra* and *Symphyomitra.* The third line, beginning with *Lophozia,* leads through *Sphenolobus* to the great family Lejeuniaceæ, and to the characteristic genera *Porella* and *Frullania,* which may be considered to represent the most perfectly developed characters of the whole order.

## THE ANTHOCEROTALES

The Anthocerotales, Cavers's fifth order of Hepaticæ, comprise a comparatively small number of liverworts of very peculiar structure, and very readily distinguished from all other plants. The differences between them and the other liverworts are so marked that they are sometimes considered a class—Anthocerotes—coordinate, on the one hand, with all the other liverworts, on the other with the true mosses.

The structures of the four genera which are comprised in the order are so much alike that they can all be assigned without question to a single family, Anthocerotaceæ.

The gametophyte is of simple structure, and all the cells much alike, each as a rule containing a single large chromatophore resembling that of many green algæ. The reproductive organs, both archegonia and antheridia, show certain peculiarities, which in some ways have their nearest approximation among the lower ferns, and in connection with the characters of the sporophyte suggest a real connection between the ferns and the Anthocerotalea.

The sporophyte differs much from that of the other liverworts. In all of the Anthocerotacea, except possibly some species of *Notothylas,* the spore-producing tissue all arises from the outer region (amphithecium) formed by the first periclinal divisions in the capsule, and much the greater part of the tissue of the sporophyte remains sterile. In all cases a large foot is present, and above it a zone of actively dividing cells is present, which may retain its activity for several months, so that the sporophyte may attain a length of 10 centimeters or more. As the outer tissues are in most cases well provided with chlorophyll, and sometimes with stomata, a complete photosynthetic apparatus is established much in advance of anything found in the other Hepaticæ.

This long-continued growth of the sporophyte is associated with a central strand of conducting tissue (columella), which is reminiscent of the axial vascular bundle of the young sporophyte of some of the lower ferns to which the sporophyte of *Anthoceros* shows the closest resemblance known in the Bryophyta.

Within the Anthocerotaceæ is an interesting series connecting the small sporophyte of *Notothylas* with its relatively large development of sporogenous tissue, and the large sporophyte of *Anthoceros* with a small amount of sporogenous tissue and a highly developed photosynthetic system.

It is, at present, impossible to say whether or not the type of *Notothylas* is a reduced one. Cavers believes it is a primitive type from which the more highly developed genera, culminating in *Anthoceros,* have been derived. He is inclined to minimize the importance of certain striking features, *e. g.,* the peculiar chloroplasts and the endogenous antheridia, and thinks the differences between the Anthocerotales and the other liverworts are not sufficient to warrant their separation into distinct classes. He considers the columella of the Anthocerotaceæ may be connected with the true liverworts through the Sphærocarpales, which they resemble in a number of particulars.

It may be noted, in passing, that there is a possibility of a connection of the Anthocerotaceæ with some of the lower Marchantiales. The Targioniaceæ, especially *Cyathodium,* for example, show some interesting analogies in the sporogonium with *Notothylas,* and the gametophytes also agree in the presence of large lacunæ, and the chromatophores of *Cyathodium* are also of unusual size.

Cavers's conclusions may be summarized as follows: From some common ancestral form, "Sphæro-Riccia," two lines of development diverged, one leading to the Marchantiales, the other to the Sphærocarpales, which in turn gave rise to the lower Jungermanniales. From some member of the latter, perhaps *Fossombronia,* all of the leafy liverworts arose. Somewhere near the Sphærocarpales it is assumed that the Anthocerotales branched off.

We are inclined to believe that some modifications of this arrangement are likely to be made. It is quite possible that *Fossombronia* should be removed from the Jungermanniales, and associated with the Sphærocarpales; and if Cavers's assumption is correct, that the leafy liverworts (Acrogynæ) have arisen from a prototype resembling *Fossombronia,* this would entirely divorce the two great divisions of the Jungermanniales.

It is doubtful whether the derivation of the Anthocerotaceæ from the Sphærocarpales will be generally accepted. For the present, at least, the order must be regarded as a very isolated one, and perhaps best considered to represent a distinct class.

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## INVERTEBRATES

UNDER the able leadership of Professors Zeigler and Woltereck there is appearing from Klinkhardt's press in Leipzig a series of excellent small monographs of familiar animals designed for the student, teacher, investigator and amateur who desires to secure a brief but authentic account of the results of systematic, histological, morphological, anatomical and embryological investigations on representative types of animals. Two volumes have already appeared, the frog by Dr. Hempelmann, and the rabbit by Dr. Gerhardt, and the series of invertebrates has been introduced by two volumes, volume 3 of the series on "Hydra und die Hydroiden" by Dr. Steche, of Leipzig, and volume 4 by Professor Meisenheimer, of Jena, on "Die Weinbergschnecke."

Dr. Steche's volume is designed not merely as a monograph on *Hydra* along the lines on which the series is planned, but adds to these the features of an introduction to the experimental treatment of biological problems as offered by the lower animals. *Hydra* is an exceptionally favorable subject for this treatment by virtue of its hardiness, ease of obtaining and of maintenance, and simplicity of structure. Few invertebrates have served as a basis of so many and so varied experimental tests and have been the object of so many investigations as *Hydra*. With this wealth of results before him it is not to be wondered at that this modest volume is open to the charge of some sins of omission. The choice of topics treated is, however, most catholic and this author has wisely avoided controversial difficulties. The histological and embryological sections are less

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[1] "Monographien einheimischer Tiere," Herausgegeben von Professor Dr. H. E. Ziegler, Stuttgart, und Professor Dr. R. Woltereck, Leipzig, Bd. 3; "Hydra und die Hydroiden. Zugleich eine Einführung in die experimentelle Behandlung biologischer Probleme an niederen Tieren," von Dr. Otto Steche, vi + 162 pp., 65 figs. in text and 2 pls., M. 4, geb. M. 4.80; Bd. 4, "Die Weibergschnecke, *Helix pomatia*," von Professor Johannes Meisenheimer, 140 pp., 1 pl. and 72 figs. in text, M. 4, geb M. 4.80.